CHANGES WITH AGE IN THE PROPORTION OF THE DOMINANTS IN A BEECH-MAPLE FOREST IN CENTRAL OHIO[1]

JOSEPH D. LAUFERSWEILER
Department of Botany, The Ohio State University, Columbus 10

In considering the concepts of plant succession and the community changes that it implies, the primary principle that may be distilled is this: whatever the compositional change wrought in any given community by successional phenomena, irrespective of direction, degree, or duration, the mechanism is that of individual replacement. As a given plant dies, if the space it once occupied is assumed by another individual of another species, a compositional change has been wrought in the community pattern. When the replacements have occurred in such fashion and such number as to alter grossly the appearance of the vegetation of an area, succession is said to have occurred, and one distinct community type has been replaced by another, assuming conditions which preclude drastic alteration of the macroclimate of the region.

It would be well here to clarify the difference between the how and the why of such change in time. The mechanism of replacement is proposed here to answer the how and when. The why involves all of the effects of the varying environmental factors, micro- and macro-, reflected in the rates of processes of the individual, as determined by inherent genetic limitations, operative from the propagule to the senescent stage. It is also recognized, however, that the mechanism of individual replacement may result in no discernible change in a community's appearance, structure or composition, and so it becomes the instrument of maintenance, rather than succession. The distinction is drawn, then in whether the replacement results in like (maintenance) or dissimilar (succession) populations.

Thus when the state of self-replacement has been reached by a community, it remains in a relatively perfect to imperfect state of equilibrium with its environment. And though the community fails to substantially change through time, within such a community the meachanism of individual replacement continues, and striving to answer the question "why? " remains as staggering a task as answering the "why? " concerned with succession.

Of the various associations composing the vegetational mosaic of the Ohio till plains, the climax mesophytic association is that dominated by American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh). This community has given its name to the forest region delimited largely by the extent of Wisconsin glaciation.

Although considered one of the regional climaxes, the beech-maple community exists areally side by side with developmental communities of the region, such co-existence being brought about to a great extent by the slight topographic irregularities characteristic of the till plain. This climax community occupies well aerated portions of the region, the swamp forest developmental stages occurring in the poorly drained depressions, flat uplands and along flood plains, and the oak-hickory type on the excessively drained rises and morainal ridge tops (Braun, 1950).

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[1]Personal acknowledgements are made to John N. Wolfe. Publication No. 569, Department of Botany and Plant Pathology, The Ohio State University.

THE PROBLEM

The beech-maple community because of its mesophytic position in the developmental relationships of the regional vegetation, and because of its large areal extent originally, has been the subject of numerous investigations. Three of these in the writer's opinion appear to be outstanding. Esten's (1932) because it is the first attempt at quantitative investigation into all portions of the community, Cain's (1935) because it remains even until today the most complete quantitative investigation into the community structure *per se*, Williams' (1936) because of its unique bio-approach to the community.

One of the more interesting phenomena mentioned by all three of these investigators is the numerical superiority of beech over maple in the canopy with the situation reversed in the reproduction.

Esten (1932) in her summary, says, "It was evident in the entire area and in the large quadrats where trees above two inches in diameter were considered that beech was higher in both coverage and frequency than maple, although maple was slightly higher in density. . . . In the four meter quadrats, where seedlings and saplings under two inches in diameter were counted, a great difference was noted in the reproduction of the two species. In 1931 there were 399 individuals of *Acer saccharum* as contrasted to twenty-eight of *Fagus grandifolia.* In 1932 a count was made of the beech and maple seedlings and saplings in the same area, and the maples showed an even greater gain in the reproductive layer over the beeches. At this time there were 1433 maples and seventy-three beeches, most of these being seedlings."

Cain (1935) recording a conversation with an old resident from the Warren's Woods area, remarks: "Fifty years ago, as now, the woods were dominantly beech, but not so much so. Mr. King also emphasized the heavy maple reproduction which now attracts so much attention. He remembers this as characteristic since his first acquaintance with the woods."

Williams' (1936) writing of the reproduction within a beech-maple area where trees 3.5 in. and over did show an almost 2:1 ratio in favor of beech, says: "The seeding of both beech and sugar maple is periodically abundant, but beech seedlings do not survive as well as those of sugar maple in the early stages of their development. In one area approximately 25 ft. sq., 12 beech trees of from 2 to 4 season's growth were counted, while the number of sugar maples of the same ages in the same area was estimated to be in the neighborhood of 3,000, a proportion of 1 beech to 250 sugar maples. Yet the high mortality of young sugar maple saplings later seems to more than make up for this difference in the early years of development."

Braun (1950), in her summary of the association type, states that "beech is usually the most abundant canopy tree, while sugar maple dominates in the understory."

An interesting facet of this consideration involves speculation as to a possible increase in the importance of maple in the canopy in view of its great numerical superiority in youthful stages. As indicated from the quotation above, Williams (1936) is of the viewpoint that progressive changes occur from the young trees to the mature, and that the dominance of beech will be maintained indefinitely under present day conditions. He cites further evidence from conversation with a resident in the area of his investigation, in which the resident, Mr. Percy Parker, points out that areas now clear of understory trees were densely crowded with sugar maple saplings when he was a boy. Esten (1932) indicates that although no definite conclusions may be drawn, evidence so far indicates that maple may be succeeding beech. Cain (1935) indicates that "it does not seem to the writer that we are yet justified in saying that maple is generally tending to increase in importance over beech in these western areas now dominated by beech, but this

FIGURE 1. Overall View of the Problem Area Indicating Dominance of Beech in the Canopy Stems.
FIGURE 2. Close View of Canopy Beech and Root Sprouts.

successional tendency is strongly indicated for several places known to the writer in Indiana and Michigan."

It seems unwise to postulate an increasing role of importance for maple in the canopy, in view of the testimony offered by Williams and Cain, and in addition, the lack of known communities within the boundaries of what has been delimited as a Beech-Maple region, that show numerical superiority of sugar maple to beech in the canopy layers. Indeed, only in the northern transition zone between the Deciduous Forest and Hemlock-Hardwood regions, are there communities where sugar maple is numerically dominant; these are transitional in nature, reflecting the varying ranges of environmental control in such areas.

As suggested earlier, then, a two-fold problem concerning this change in dominance remains: When does beech attain ascendancy? And why? It is with the former question that this brief study is concerned.

LOCATION OF STUDY AREA

In order to gain some awareness of the nature of the change occurring in the relative proportions of beech and maple as they pass through the various stages of their communal existence in the development from seedling to dominant, this investigation was undertaken. A "typical" area of Beech-Maple forest was selected to obtain information on the proportions of beech and maple at various age and height levels.

This area, which DeSelm (1952) has described in greater detail, lies "at the western edge of a level to gently undulating Late Wisconsin till plain, between Black Lick Creek and South Fork of the Licking River. It is in northwestern Etna Township, Sec. 3, T 16 N, R 20 N, Licking County, as noted on the Thurston, Ohio, U.S.G.S. quadrangle.

"The elevation varies from about 1080 ft. along a slight ground swell at the western edge of the forest, to 1070 ft. along an intermittent, south-flowing stream which bisects the forest. The terrain thus slopes gently east and south.

"Two soil types form a mosaic in the . . . area, . . . the Marengo silty clay loam and the Bennington silt loam, both derived from glacial drift largely composed of sandstones and shales. . . . . The former developes on flat upland areas having poor internal drainage and abundant organic matter. Internal drainage of Bennington is better than that of Marengo although accumulation of organic matter is less. It occurs on the undulating uplands. . .

"Beech (*Fagus grandifolia*), constituting over half the canopy, dominates the vegetation in the sampling area" (fig. 1).

The counts, reported in the present paper, were made during the prevernal season of 1954.

METHODS AND RESULTS

An area 100 ft. sq. was chosen in which there were 8 beech and 3 maple crowns in the canopy (72.73% beech; 27.27% maple). In all there were 19 trees over 3 in. dbh; 9 beech (47.37%), 4 maple (21.05%), 4 elm (21.05%) and 2 ash (10.53%). One beech was in the immediate understory. One of the four maples was dead, with the bole still standing.

In addition, within the 10,000 sq. ft. area, 10 smaller quadrats, 3 ft. sq., were randomly distributed in order to count the low beech and maple seedlings, one and two years old.

All beeches and maples older than this were counted within the entire area of the large quadrat. For the younger stages, ages were determined by counts of the terminal bud scale scars, for the older ones annual ring counts were used. The distribution of individuals with age is presented in table 1. The counts from the small quadrats have not been converted to an equal area basis, since the percentages would not be effected, and these are used to indicate the trends. It should be indicated that beech reproduces not only by seed but also by means of sprouts arising from the roots (fig. 2). Such sprouting was not observed to occur on maples. Five of the 8 canopy beech exhibited this sprouting phenomenon, one having 16 sprouts, another 13, another 9, and two had one each. These have been included in the data, and their effect on the counts noted in the table.

Beech does not gain a persistent numerical ascendency until the 40-year group is reached. In the earlier ages, the maple greatly exceeds the beech, save for the anomalous condition in the 2 and 3-year old groups. When root sprouts of beech are eliminated from consideration maple is numerically superior in all age group-

TABLE 1

Proportions of beech and maple under canopy level at various ages in a "typical" Beech-Maple Forest in Central Ohio

					Without Root Sprouts		
Age	No. of Maple	No. of Beech	% Maple	% Beech	No. of Beech	% Maple	% Beech
1	482	96	83.39	16.61	96	83.39	16.61
2	7	10	41.18	58.82	10	41.18	58.82
3	8	10	44.44	55.56	10	44.44	55.56
4	10	7	58.82	41.18	7	58.82	41.18
5	14	9	60.87	39.13	9	60.87	39.13
6	21	10	67.74	32.26	10	67.74	32.26
7	28	11	71.79	28.21	11	71.79	28.21
8	24	11	68.57	31.43	10	70.59	29.41
9	23	7	76.67	23.33	7	76.67	23.33
10	31	6	83.78	16.22	6	83.78	16.22
11	25	6	80.65	19.35	5	83.33	16.67
12	27	9	75.00	25.00	6	81.92	18.18
13	27	8	77.14	77.14	7	79.41	20.59
14	18	9	66.67	33.33	8	69.23	30.77
15	20	8	71.43	28.57	7	74.07	25.93
16	12	7	63.16	36.84	6	66.67	33.33
17	13	9	59.09	40.91	6	68.42	31.58
18	12	7	63.16	36.84	3	80.00	20.00
19	14	6	70.00	30.00	4	77.78	22.22
20	10	7	58.85	41.18	3	76.92	23.08
21	9	5	64.29	35.71	4	69.23	30.77
22	7	5	58.33	41.67	4	63.64	35.36
23	9	2	81.82	18.18	1	90.00	10.00
24	10	3	76.92	23.08	2	83.33	16.67
25	2	2	50.00	50.00	1	66.67	33.33
26	4	1	80.00	20.00	0	100.00	00.00
27	3	0	100.00	00.00	0	100.00	00.00
28	2	2	50.00	50.00	0	100.00	00.00
29	3	2	60.00	40.00	0	100.00	00.00
30–40	8	5	61.54	38.46	1	88.89	11.11
40–70	2	4	33.35	66.67	0	100.00	00.00

ings (table 1). The average heights of the individuals in the age groups are indicated in table 2. Beech is consistently taller than maple in each group, indicating a faster vertical growth rate. The oldest tree of this grouping, however, is a 63 year old maple, 14.3 ft. tall, while the oldest beech, 50 years, is 48.8 ft. tall.

Data are presented in table 3, grouping the two species according to height classes. In the lower height classes maple is again numerically superior but proportionally decreasing with increasing height. After 3.5 ft., however, numbers of beech exceed those of maple and continue to do so with the successively taller groups. Without considering root sprouts beech still attains the majority, but not to as great an extent, and is absent from the tallest groupings (> 102 in.).

CONCLUSIONS

Data gathered in this study indicate that the transference of numerical dominance from maple to beech occurs in the age group between 40–70 years. In height grouping the changeover occurs at the 3.5 ft. level and beech superiority becomes stronger with increasing height. It is unfortunate that the critical age group is one in which the sample size is small. Data from other investigators also show this absence of numbers in the critical group (table 4).

TABLE 2

Average height of beech and maple for each of the various age groups

Age	Average Height (Inches) Maple	Beech
1	3.5	5.0
2	5.1	5.4
3	6.1	7.0
4	7.9	8.4
5	9.7	11.4
6	9.8	11.8
7	9.6	15.9
8	10.2	14.8
9	10.3	22.0
10	10.8	26.0
11	11.3	24.2
12	11.5	24.9
13	11.1	25.1
14	14.1	32.9
15	14.7	30.9
16	14.9	43.5
17	15.7	39.8
18	16.4	42.9
19	20.5	37.7
20	24.0	33.7
21	28.0	39.0
22	24.5	52.2
23	26.5	106.3
24	34.1	53.7
25	41.0	85.0
26	27.2	87.0
27	28.7	......
28	33.5	96.0
29	28.5	69.5
30	35.0*	70.0
31	31.0*	......
33	32.5	121.0*
35	48.5	67.0
36	48.0*	......
38	25.0	127.5*
40	......	204.5*
45	......	129.5
50	150.0*	585.0*
63	172.0*	......

*Based on one individual.

It would seem from study of both age and height data, that the most important factor in the maintenance of beech dominance in the canopy is the ability of beech to reproduce by root sprouts. If these are omitted from consideration in both age and height data then maple has clearer dominance in the older and taller understory groups. Consequently root sprout presence not only re-establishes beech in these groups, but is responsible for the majority it shows. Williams

(1936) also indicates the possible importance of root sprouting and this phenomenon alone is responsible for some dense stands of beech in Pennsylvania, according to Illick and Frantz (1928).

This investigation was undertaken to indicate at what age, and in what height levels, the changes in proportion between beech and maple have occurred, resulting in a beech-maple canopy, after having exhibited maple-beech stages in the reproduction. No definite study has been undertaken to indicate why this phenomenon

TABLE 3

Proportions of beech and maple under the canopy, according to height groups.

Height (inches)	No. of Maple	No. of Beech	% Maple	% Beech	No. of Beech	Without Root Sprouts % Maple	%Beech
0–6	540	47	91.99	8.01	47	91.99	8.01
6–12	224	46	82.96	17.04	46	82.96	17.04
12–18	63	22	74.12	25.88	19	76.83	23.17
18–24	34	26	56.67	43.33	25	59.65	40.35
24–30	25	21	54.35	45.65	16	60.98	39.02
30–36	24	17	58.54	41.46	13	64.86	35.14
36–42	17	18	48.57	51.43	14	54.84	45.16
42–48	2	7	22.22	77.78	4	33.33	66.67
48–54	1	8	11.11	88.89	7	12.50	87.50
54–102	0	18	00.00	100.00	10	00.00	100.00
102–	2	9	18.18	81.82	0	100.00	00.00

TABLE 4

Proportions of beech and maple from data of Cain (3) *and Esten* (4). (*Compiled by Cain* (3)).

Classes	No. Beech	No. Maple	Ratio
Cain			
Under 1 ft. high	156	3,923	1 : 25
Under 1 in. d.b.h.	230	1,055	1 : 14
1 in. d.b.h.	38	61	1 : 2
2 in. d.b.h.	8	12	1 : 1.5
3 in. d.b.h.	1	3	1 : 3
4–9 in. d.b.h.	11	2	5.5 : 1
Esten			
Under 2 in. d.b.h.	224	3,392	1 : 4
2 in.	10	25	1 : 2.3
4 in.	3	12	1 : 4
6 in. or over	24	2	12 : 1

occurs. Speculation as to some factors involved might indicate sporadic light seeding of beech, and the use of beech nuts as forage by many of the small animals inhabiting such a forest of importance in determining the maple dominance in the youthful stages; the faster vertical growth rate of beech, variation with age in the photosynthetic-respiratory ratios, differing frost resistance, and others as determining factors in the subsequent establishment of beech numerical superiority. Of interest from the above data is the temporary majority of beech in the two and three year groups. This may indicate a heavy mortality of one year old maple seedlings, especially during drought years such as occurred in the region just prior to the present study. If the "why" answer is to be found it may well lie in a study of such extremes, for it is an ecological truism that extremes rather than the means are the important determiners of species limits, both geographical and communal. It has been indicated, that for this area, beech root sprouting has been a deciding factor for beech dominance in late stages; why such sprouting occurs on some beeches and not on others, is unknown to the author.

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